

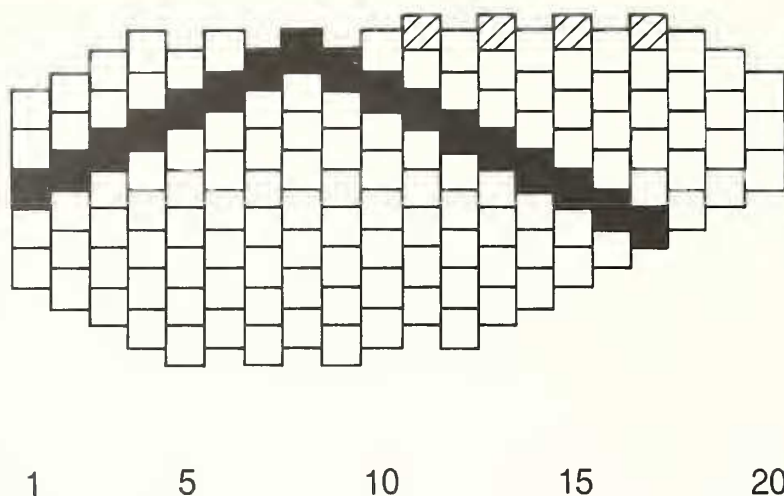
VARIATION IN THE EYES OF THE SILURIAN TRILOBITES *EOPHACOPS* AND *ACASTE* AND ITS SIGNIFICANCE

by A. T. THOMAS

ABSTRACT. Among the compound eyes of trilobites, the most remarkable are the schizochroal type of the suborder Phacopina. As well as representing an ancient visual system of probably unique kind, schizochroal eyes show patterns of variation in lens distribution which have figured in discussions of possible dimorphism and polymorphism in trilobites species, and have been used by some authors as taxonomic characters. *Eophacops musheni* is a common species in the British Wenlock, and variation in the lens pattern on the visual surface is described from about 40 well preserved specimens. Adults typically have 19 or 20 files of lenses, and two cases are described of individuals with 20 files in the left eye and 19 in the right. Comparable cases occur in *Acaste*. Dimorphism in the visual surface of *A. downingiae* is doubtful. The new data on the variation of the visual surfaces of *E. musheni* and *A. inflata* indicate that visual surface morphology provides a reliable guide to species identity only in some cases. They also allow Clarkson's developmental model for the visual surface to be extended to imply that the initial length of the section of the generative zone actively producing lenses was variable, and that lens emplacement was initiated at different times relative to the descent of the generative zone in different individuals. If development of a lens was controlled by the distance from adjacent lens centres, and given that lenses are round and that emplacement began in a single horizontal row, hexagonal close packing and the development of dorso-ventral files result automatically. Cubic close packing could be produced by modifying the spacing factor in successive horizontal rows. The number of dorso-ventral files of lenses and their relative height are controlled by the length of the active section of the generative zone and its pattern of growth. The existence of individuals with eyes differing in the number of files demonstrates that file number is a consequence of a developmental programme, rather than being under immediate genetic control. Variation in the timing of termination of lens emplacement accounts for the observed variation posteriorly and near the base of the visual surface.

THE calcite compound eyes of trilobites, notable for being the oldest preserved visual system, have been the subject of scientific investigation for more than a hundred years. The structures which originally underlay the lentiferous visual surface are unknown, thus limiting our understanding of the animals' vision. Nevertheless, the morphology and function of trilobite eyes have been the study of intensive investigation in recent decades (see Clarkson 1975, 1979 for reviews). Two principal types of eye morphology have been distinguished: the more primitive holochroal eyes, characteristic of most trilobite groups, and the schizochroal type of the suborder Phacopina. A possible third kind of eye, which has at least some features in common with the schizochroal type, occurs in eodiscid trilobites, but its distinctiveness remains to be confirmed (see Zhang and Clarkson 1990, p. 912).

Schizochroal eyes differ from holochroal ones in possessing separated, thick, biconvex lenses, which are relatively large (sometimes < 1 mm across; Clarkson 1979, p. 12), compared with the average lens diameter of 100 μm in holochroal eyes (Horváth *et al.* 1997, p. 233) and circular in plan view (square lenses occur in some trilobites with holochroal eyes: see Clarkson 1975, fig. 5k, p. 17; Fortey 1997, p. 403). All schizochroal lenses are doublet structures: an upper lens unit composed of calcite with the c-axis orientated perpendicular to the visual surface, underlain by an intralensar bowl. The aplanatic character of the doublets corrected for spherical aberration (Clarkson and Levi-Setti 1975). It is possible, however, for spherical aberration to be corrected by singlet lenses of the appropriate shape. Horváth (1996) argued that a possible function of the intralensar bowl might



TEXT-FIG. 1. Schematic representation of visual surface in a paralectotype of *Eophacops musheni* (Salter, 1864) (BU 59a), showing the terminology used in the text. Front of eye is to left; numbers below drawing denominate individual dorso-ventral files, counting from the front. Black boxes indicate single examples of ascending and descending diagonal rows; oblique shading indicates accessory upper horizontal row.

be reflectivity reduction and enhanced light transmission. The overall features of the schizochroal eye suggest that a unique kind of visual system might be represented, which acted as an aggregate of simple eyes rather than being directly comparable to the compound eyes of most other arthropods (Fordyce and Cronin 1993; Horváth *et al.* 1997). The geometrical arrangement of lenses on the visual surface is such that schizochroal-eyed trilobites may have possessed stereoscopic vision throughout the visual field (Stockton and Cowen 1976).

Partly because they are such striking features, eye morphology and the pattern of lens distribution have figured in discussions concerning possible dimorphism and polymorphism in various phacopine species, and have sometimes been used in separating genera and species. Often, however, the available material has been poorly localized, and sample sizes have been small. Continuing studies of trilobites from the British Wenlock have included examination of eight named species of the phacopid genera *Eophacops* and *Ananaspis*, and the acastomorphs *Acaste*, *Acastoides* and *Acastocephala*. Full descriptions of the species will be published in the next part of my monograph (1978, 1981, continuing) of the fauna. This paper describes the pattern of eye lens variation in *Eophacops musheni*, where the number of suitably preserved specimens is relatively large and the material is tolerably well localized. Additionally, examples of *E. musheni* and *Acaste inflata* are described in which the right and left eyes of individual specimens show different patterns of lens distribution. The developmental significance of these abnormalities, and the use of eye lens patterns in taxonomy and the discrimination of dimorphs and polymorphs, are reviewed below.

Terminology and eye lens diagrams. Terminology follows Clarkson (1966a, p. 2, text-fig. 1). Lens plots for the species (Text-fig. 1) generally follow the method of Clarkson and Tripp (1982, fig. 6, p. 293), a development of Campbell's (1977, p. 40) system, which allows the characteristic hexagonal close packing to be represented (also see Howells 1982, p. 42). For the reasons explained in the text, however, positionally equivalent lenses are first identified at the front of the visual surface rather than at the back. The characteristic arrangement of lenses in dorso-ventral files and horizontal rows is preserved. The additional arrangement of lenses in ascending and descending diagonal rows, which is a geometrical consequence of the packing arrangement, is also represented.

Stereographic plots are needed if it is desired to represent the sizes of lenses and their separation with minimal distortion (Clarkson 1996a, p. 7).

SYSTEMATIC PALAEOLOGY

Remarks. The species considered here will be revised fully elsewhere. Because none of them has been described in recent years, however, sufficient taxonomic data are given to make my concept of the species clear. Descriptive details refer to aspects of eye morphology only.

Order PHACOPIIDA Hawle and Corda, 1847
 Suborder PHACOPINA Hawle and Corda, 1847
 Family PHACOPIDAE Hawle and Corda, 1847
 Subfamily PHACOPIDELLINAE Delo, 1935

Genus EOPHACOPS Delo, 1935

Remarks. This name has been conserved by the International Commission on Zoological Nomenclature in Opinion 1846 (*Bulletin of Zoological Nomenclature*, 53 (for 1996), p. 205; see Owens and Thomas 1995).

Eophacops musheni (Salter, 1864)

Plate 1, figures 1–5, 7–8; Text-figures 1–4, 6

- v*.1864 *P. (Phacops) Musheni*, n. sp., Salter, p. 23, pl. 2, figs 7–12.
- .1966b *Phacops musheni* Salter 1864; Clarkson, p. 77, pl. 1.
- .1967 *E. musheni* (Salter); Campbell, p. 38, pl. 12, fig. 20.
- .1985 *Eophacops musheni* (Salter, 1864); Ramsköld, p. 28, pl. 5, figs 2–3, 5–7, text-fig. 4B.

Material, localities and horizons. The syntypes include BU59a–c and two untraced specimens (Morris 1988, p. 2), from the Coalbrookdale Formation (?), Malvern, Hereford and Worcester; NHM 58898, It9660, from the Much Wenlock Limestone Formation (Homerian), Dudley, West Midlands. Salter's figures are partly restored: the closest match with an actual specimen is between his plate 2, figure 9 and BU59c (Pl. 1, fig. 5). That specimen shows the cephalic doublure as well as the dorsal morphology, and is here selected as lectotype. There is some doubt about the horizon from which the BU59 specimens came. Salter gave the horizon as 'Wenlock Shale' (= Coalbrookdale Formation), but the BU catalogue records it as 'Woolhope Shale' (= Wych Beds, Telychian). The specimens were originally part of the Ketley Collection, but no primary documentation relating to them survives. If the BU catalogue is correct, the range quoted for this species by Thomas *et al.* (1984, fig. 23, p. 52) is extended downwards. Several other typically Wenlock species are recorded from this horizon also (Thomas *et al.* 1984, p. 54). The Dudley syntypes probably came from the storm-generated obrution deposits which occur towards the top of the Nodular Beds Member of the Much Wenlock Limestone Formation (see Dorning (1983) for formalization of Butler's (1939) lithostratigraphy).

There are many good, articulated (commonly enrolled) specimens of this species in the major British palaeontological collections. Most are from the Coalbrookdale Formation of the Malvern area or the Much Wenlock Limestone Formation of the West Midlands inliers or Malvern. Similarities in preservation suggest that most of the specimens came from a small number of horizons.

The species also occurs in the Wenlock of Gotland. In describing that material, Ramsköld (1985, p. 30) noted contrasts between the smaller Malvern specimens and the larger ones from Dudley figured by Salter, suggesting that he might have confounded two *Eophacops* species. Study of all the available British material suggests that Salter was correct in assigning his specimens to a single species.

Description. Because Ramsköld (1985) suggested that separate species might be represented in the Dudley and Malvern areas, data relating to specimens from the two localities are plotted separately (Text-fig. 2A–B). A two-tailed version of the non-parametric Mann–Whitney test indicates that the samples do not significantly differ from each other in size ($U = 55.5$; a significant difference at the 5 per cent. level requires $U < 42$). The overall morphology of the visual surface is very similar in the samples from the two localities. Some Dudley specimens

have an additional lens at the base of each of files 1–4 and at the top of files 5 and 8. At both localities specimens have either 19 or 20 files (Text-fig. 3): the Malvern sample has a higher proportion with 19. A one-tailed Mann–Whitney test shows that the number of files present is not directly correlated with specimen size ($U = 79.5$; a significant correlation at the 5 per cent. level requires $U < 48$).

The minimum number of lenses is 103; the maximum number preserved is 140 (allowing for preservation, < 144 may have been present originally). The lenses shaded in files one and two in Text-figure 2 occur in all specimens, and the distribution of the other lenses is plotted accordingly. At the maximum height of the eye, files of six (rarely), seven or eight lenses alternate with seven, eight or nine respectively. The material from the Wenlock of Gotland (Ramsköld 1985, p. 25, fig. 4B) shows a pattern of variation which falls within that described here. All those specimens had 20 files.

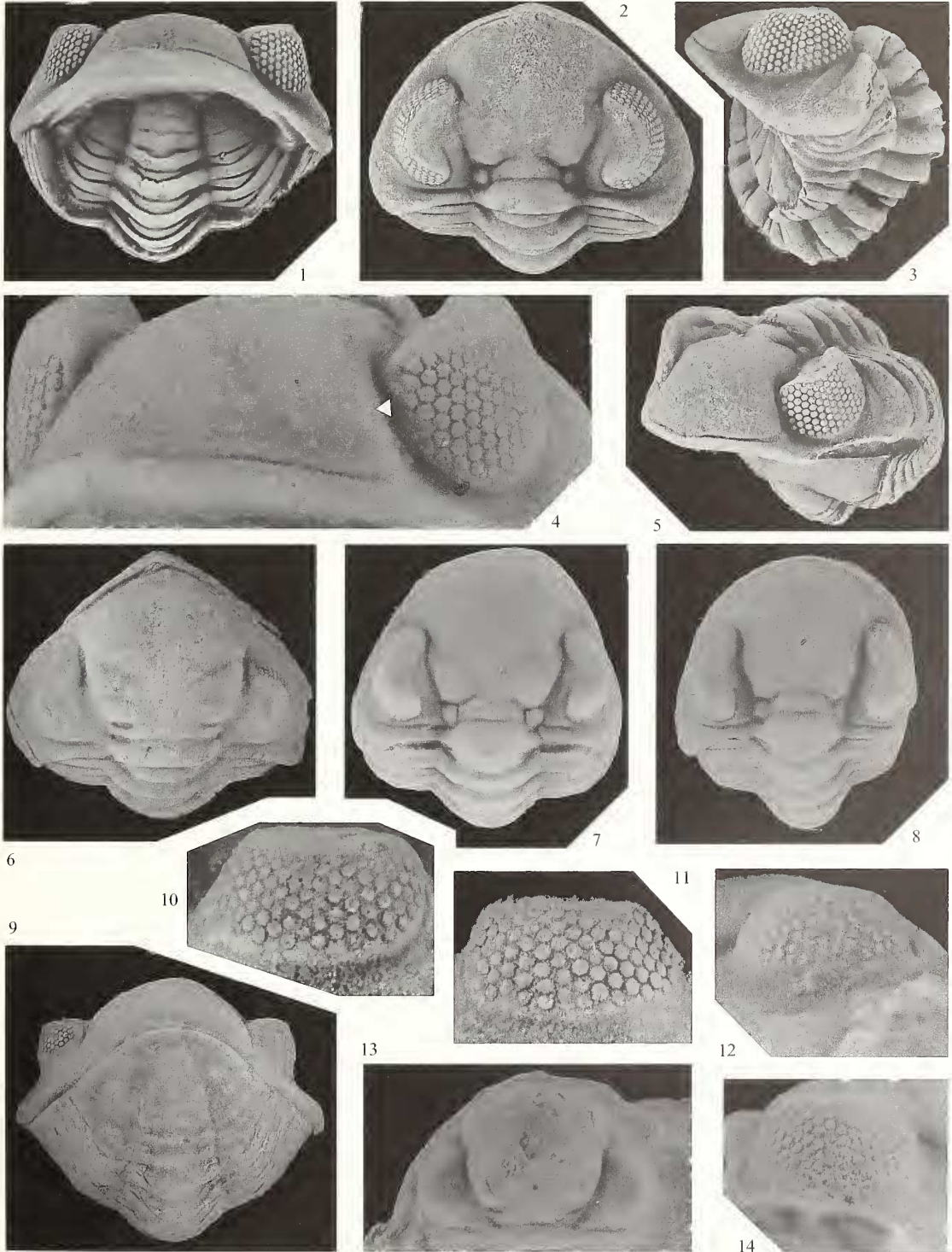
A single Malvern specimen (Pl. 1, fig. 4; Text-fig. 4B) has 21 files in its left eye. Comparison with other specimens suggests that the additional file, which contains just one lens, lies in a position which might be termed file '0'. The right visual surface is not uniformly well preserved, and a full lens count is impossible. It is well preserved anteriorly, and no single lens in this position is seen. A small depression at the anterior margin of the right visual surface may mark its position, however. Alternatively, the two eyes may have been asymmetrical in this regard. There are two specimens which certainly show different numbers of files in each eye (Text-fig. 4C–D). The right eye of OUM C16680/1 has 19 files whilst 20 occur in the left. Slight damage to the left eye makes an exact lens count impossible, but the additional file seems to occupy the position indicated by the crosses in Text-figure 4D. OUM C16680/3 (Text-fig. 4D) shows a similar posterior extension, also at the back of the left eye. There is no measurable difference in the exsagittal lengths of the eyes on the right and left sides of these specimens, but the minor distortion suffered by both makes minor differences in length impossible to establish reliably (Pl. 1, figs 7–8).

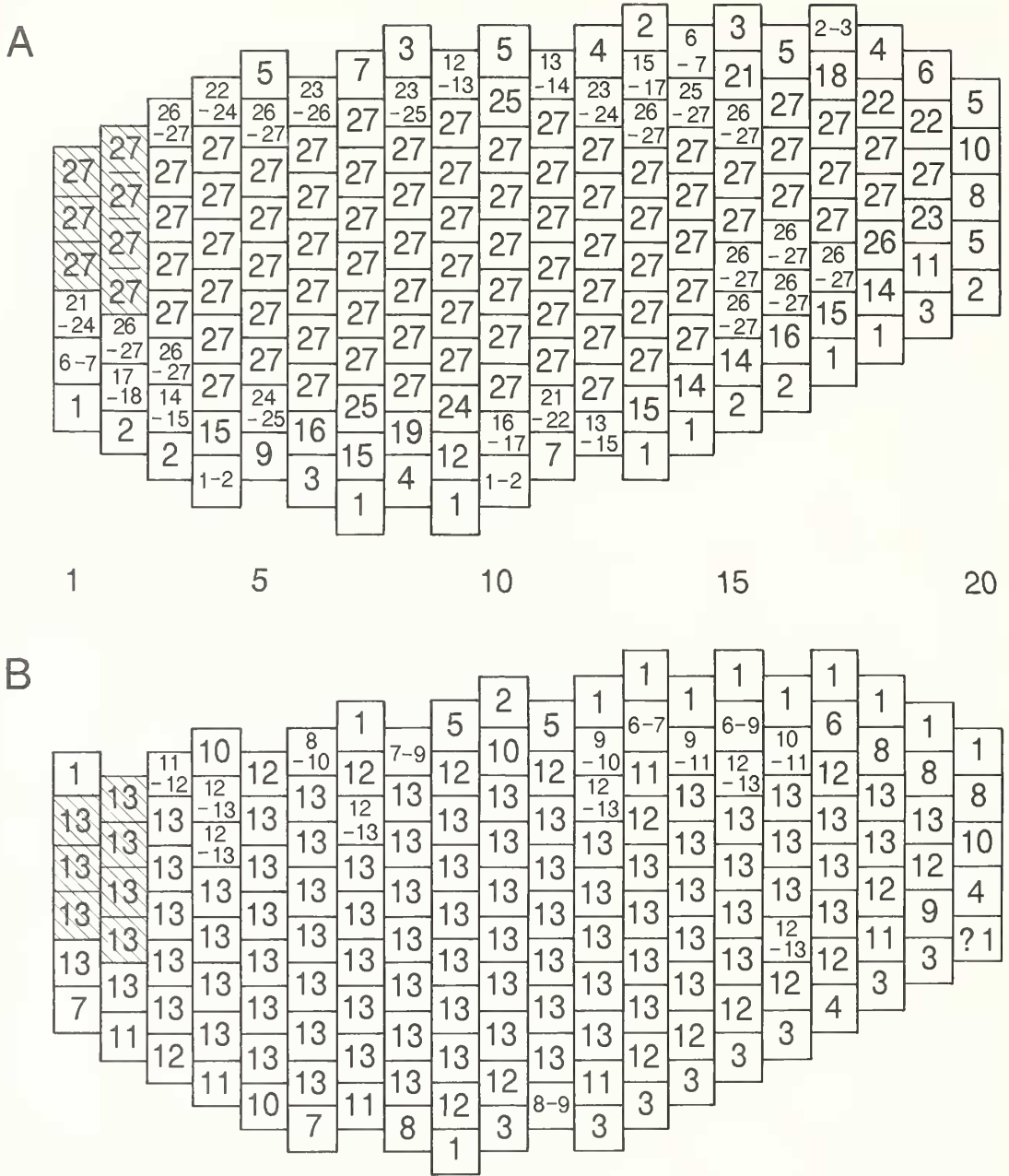
Remarks. Most variation in the pattern of lens distribution in *E. musheni* occurs dorsally, ventrally and posteriorly (Text-fig. 2): only occasionally is the front of the visual surface affected. A similar pattern of variation was noted in Devonian phacopids by Campbell (1977, p. 40), and is documented also for *Acernaspis superciliexcelsis* from the Scottish Llandoverly (Howells 1982, text-fig. 8, p. 42), and for Silurian *Eophacops* species from Gotland (Ramsköld 1985, fig. 4, p. 25). In describing material of the Ordovician *Calyptaulax brongniartii*, Clarkson and Tripp (1982, fig. 6, p. 293) noted that populations from different localities differed in the pattern of lens distribution. Comparable variation is seen in samples of *Eophacops sprogensis* from Gotland (Ramsköld 1985, fig. 4C–E). As described above, however, consistent differences between the Dudley and Malvern samples of *E. musheni* are small. This could be due to the averaging effect of combining populations from several separate original collections.

With one exception, the eyes of *E. musheni* have 19 or 20 files of lenses. The two specimens which possess 20 files in their left eyes and 19 in their right are notable in this context. There is no obvious sign of injury, yet the variation in file number between the two sides of the same specimen is comparable with that occurring between individuals in the population as a whole. Specimens of *Acaste* showing comparable asymmetries are described below.

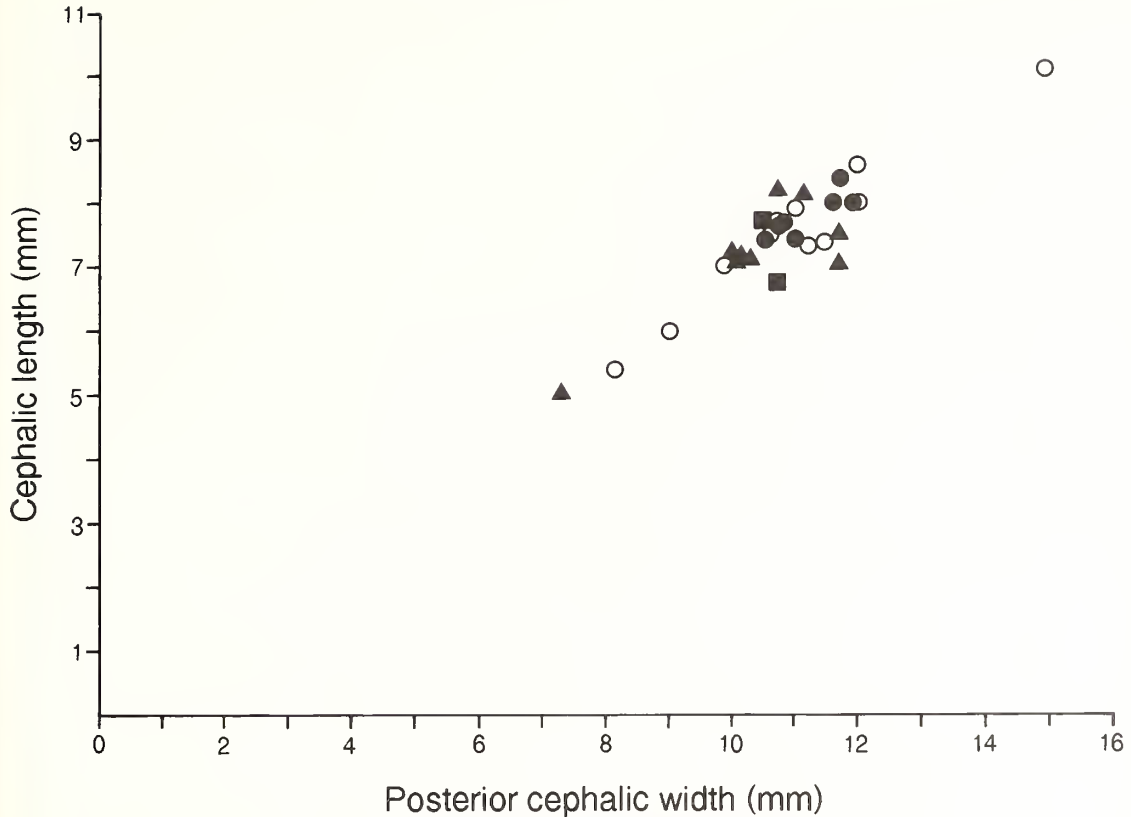
EXPLANATION OF PLATE 1

- Figs 1–5, 7–8. *Eophacops musheni* (Salter, 1864); Coalbrookdale Formation (?), Malvern district, Hereford and Worcester. 1–3, paralectotype, BU 59a; anterior, palpebral and left lateral views; $\times 4$. 4, OUM C16880/2; slightly oblique anterior view of part of cephalon; arrowhead indicates lens comprising file '0' (see text for details); $\times 10$. 5, lectotype, BU 59c; oblique anterolateral view; $\times 4$. 7, OUM C16680/1; palpebral view; $\times 4$. 8, OUM C16680/3; palpebral view; $\times 4$.
- Figs 6, 9–11. *Acaste inflata* Salter, 1864; lectotype, OUM C9; Much Wenlock Limestone Formation, Ledbury Railway Tunnel, Hereford and Worcester. 6, 9, palpebral and anterior views of whole specimen; $\times 3$. 10–11, lateral views of left and right eyes; $\times 9$.
- Figs 12–14. *Acaste* cf. *inflata* Salter; NMW 27.110.G998.3; Much Wenlock Limestone Formation, Dudley, West Midlands. 12, 14, lateral views of left and right eyes; $\times 9$. 13, palpebral view of cephalon; $\times 4$.





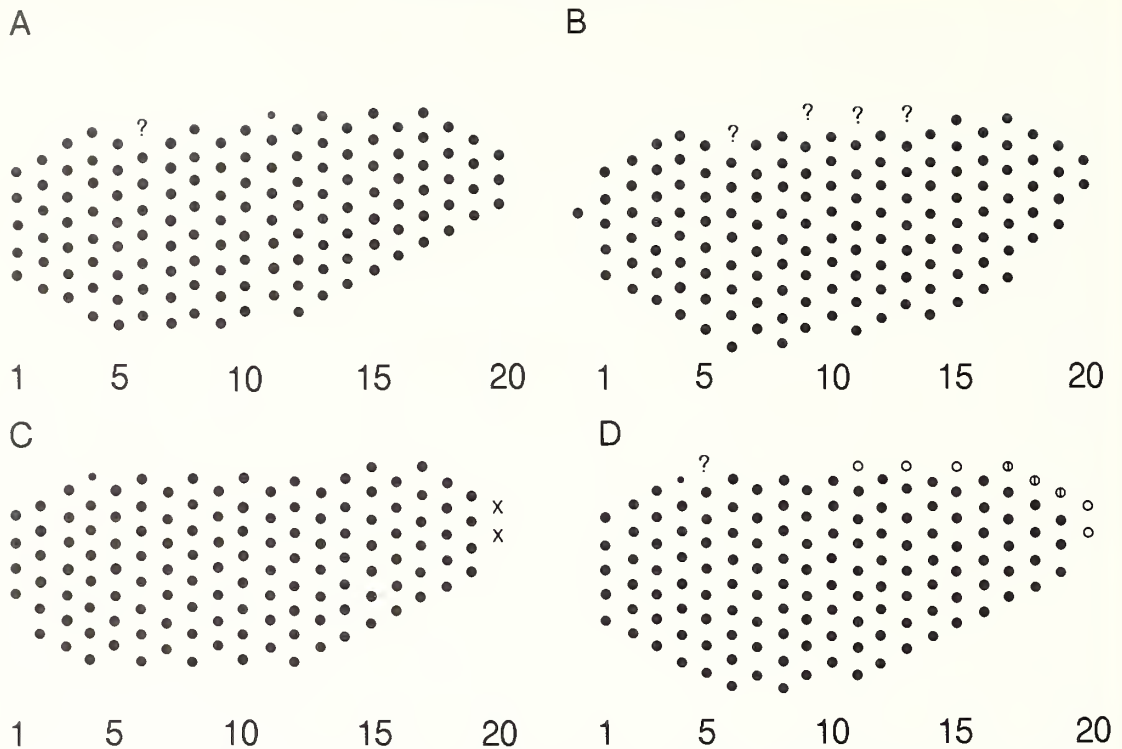
TEXT-FIG. 2. Schematic representation of visual surfaces in *Eopacops musheni* (Salter, 1864). Front of eye is to left; numbers below drawing denominate individual dorso-ventral files, counting from the front. A, sample from Much Wenlock Limestone Formation, Dudley, and Walsall (two specimens); 27 eyes of 26 specimens. B, sample from Coalbrookdale Formation (?), Malvern district; 13 eyes of 13 specimens. Numbers in boxes indicate the number of surfaces having that lens; ranges indicate uncertainty due to preservation. Positionally equivalent lenses in files 1 and 2 shaded; see text for further explanation.



TEXT-FIG. 3. Scatter diagram of cephalic length (in palpebral view) versus posterior cephalic width in 29 specimens of *Eophacops musheni* (Salter, 1864). Circles indicate Dudley specimens, triangles those from Malvern; squares are used for Walsall material. Solid symbols denote specimens with 20 files of lenses, open symbols those with 19.

In most cases where phacopine specimens with both eyes well preserved have been described, the visual surfaces are identical. Rare asymmetries have been recorded, however. Clarkson (1966a, p. 12, text-fig. 4a–b) described one specimen of *A. downingiae* with two extra lenses in the right eye and a hiatus in the centre of the left. Similar minor irregularities have been described in *Reedops* species from the Devonian of Bohemia (Clarkson 1969, pp. 195, 197). Such asymmetries could arise either from minor injuries or developmental irregularities. Ludvigsen (1979, p. 77, fig. 51c, p. 82) described a specimen of *Phacops rana*, from the Devonian of Ontario, with markedly asymmetrical eyes: the left eye is much smaller than the right, and has only about 20 lenses (compared with 67 in the right eye). Ludvigsen attributed the condition to an early injury. However, Owen (1985, p. 259) noted that the whole left cheek is reduced in size but has an otherwise normal morphology. I agree with him that this makes a genetic or developmental abnormality more likely.

There are no recent descriptions of several named species of *Eophacops* (for species list see Ramsköld and Werdelin 1991, p. 66), but good descriptions and illustrations are available for the species from Gotland (Ramsköld 1985) and Bohemia (Chlupáč 1977). Within these species, there are 18–21 files of lenses, with the maximum number per file varying from five to nine. The visual surfaces of *E. musheni* are at the larger end of the spectrum in terms of the number of lenses present. Some of the smaller-eyed species, such as *E. lauensis* Ramsköld (1985, pl. 6, fig. 5B, fig. 6F, p. 25), could be distinguished from larger-eyed forms on the morphology of the visual surface alone. In



TEXT-FIG. 4. Schematic representation of visual surfaces in *Eopachops nusheni* (Salter); Coalbrookdale Formation (?), Malvern district. Front of eye is to left; numbers below drawing denominate individual dorso-ventral files, counting from the front. A, paralectotype BU 591 (both eyes). B, OUM C16680/2 (left eye). C, OUM C16680/1 (right eye). Twenty files occur in the less well preserved left eye, the additional file apparently in the position marked by the crosses. D, OUM C16680/3: solid shading indicates presence of lens in both eyes; blank circles, presence in left eye only; circles with vertical bar, lens present in left eye but occurrence in less well preserved right eye uncertain.

other cases, however, lens patterns would provide only a more general guide to species identity, particularly given the degree of variation which occurs.

Family ACASTIDAE Delo, 1935
Subfamily ACASTINAE Delo, 1935

Remarks. The family level classification of acastomorph trilobites has been fluid ever since the group was first recognized. Edgecombe's (1993) arrangement is followed here.

Genus ACASTE Goldfuss, 1843

Type species. By subsequent designation of Burmeister (1843, p. 139); *Calymene? Downingiae* Murchison, 1839; from the Much Wenlock Limestone Formation (Homerian), Wren's Nest Hill, Dudley, West Midlands.

Acaste inflata Salter, 1864

Plate 1, figures 6, 9–11; Text-figure 5

v*.1864 *Phacops (Acaste) Downingiae* Murchison, var. γ , *inflatus*, Salter, p. 27, pl. 2, fig. 30 only.

- 1966a *A. downingiae inflatus* (Salter); Clarkson, p. 11.
 v.1966 *Acaste inflata* (Salter 1864); Shergold, p. 192, pl. 29, figs 9–16.

Lectotype. Selected by Shergold 1966, p. 192; OUM C9, complete enrolled specimen figured Salter 1864, pl. 2, fig. 30, refigured Shergold 1966, pl. 29, figs 9–14; from the Much Wenlock Limestone Formation, Ledbury Railway Tunnel, Hereford and Worcester.

Material localities and horizons. *A. inflata* is a rare species, with about 20 specimens being known from the Much Wenlock Limestone Formation of the Dudley and Walsall inliers (West Midlands) and the Ledbury area, near Malvern. Morphologically similar specimens occur in rocks of late Wenlock age in the Tortworth and Usk inliers and in the Elton Beds (lower Ludlow) of Shropshire. The BGS, NHM and OUM house most of the material.

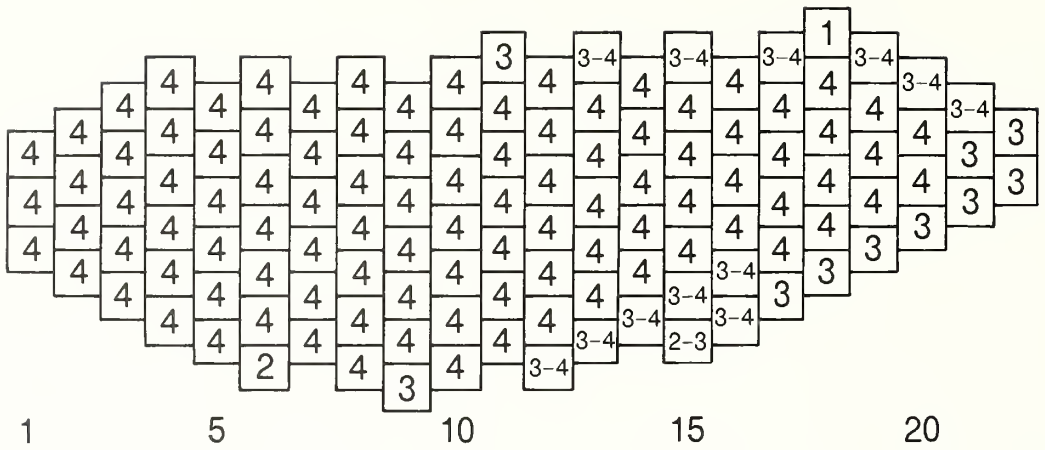
Description. Clarkson (1966a, p. 11) had no material with the visual surface preserved, but Shergold (1966, p. 192) diagnosed the species as having vertical files of seven lenses alternating with six at the maximum height of the eye. In his description (p. 193), he recorded a maximum of 130 lenses in an individual visual surface.

Text-figure 5A shows the pattern of lens distribution in the visual surfaces of four specimens of this species. There are 21 or 22 dorso-ventral files. The minimum number of lenses is 108 (allowing for preservation, 113 lenses may have been present originally); the maximum number is 122. Files 1–4 are identical in all specimens: the distribution of other lenses is plotted accordingly. The lectotype of *A. inflata* has eyes which differ in the number of files (Text-fig. 5B–C). The left eye (Pl. 1, fig. 10) has 21 files and, allowing for minor damage to the top of the visual field, compares very closely with other specimens of the species. Only 19 files occur in the right eye (Pl. 1, fig. 11), however, and the total number of lenses is 99. Files 5–9 and 11–16 contain either five or six lenses, and only file ten has seven. The right eye is *c.* 13 per cent. shorter (exsag.) than the left (Pl. 1, fig. 6; this is less evident in Shergold's 1966, pl. 29, fig. 9 because the specimen is there illustrated in occipital view, and the palpebral lobes are consequently foreshortened). In the other specimens, six is the minimum number of lenses in these files and files 4–7 have seven. Packing irregularities occur in files 7–12, but these are minor. A specimen possibly belonging to this species also has asymmetrical eyes (Pl. 1, figs 12–14; Text-fig. 5D–E). In both, files of six and seven lenses alternate at the maximum height of the visual surface. However, the left eye has 21 files and 118 preserved lenses (possibly 121 originally) whilst the right has 22 files and 126 lenses (?128 originally). In this case, the right eye is slightly shorter (exsag.) than the left (compare anterior limit of palpebral lobes relative to abaxial ends of 3S furrows on Pl. 1, fig. 13), despite the higher number of files. Packing irregularities are evident between files 15 and 19 of the right eye.

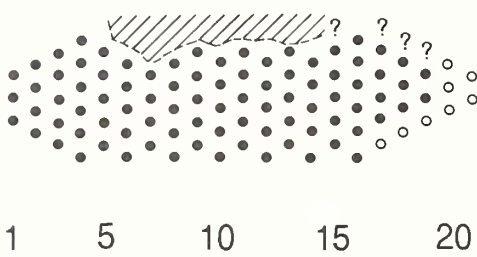
Remarks. The lectotype of *A. inflata* is notable for possessing two more files of lenses in the left eye than in the right. Increased length of the left visual field has been achieved by the development of additional files posteriorly, as appeared to be the case in comparable specimens of *Eophacops musheni*. The specimen is undistorted, and the right eye is noticeably shorter than the left, indicating that lens size and spacing have remained constant. The presence of minor packing irregularities in the right eye might indicate that the smaller number of files there reflects incomplete development of that visual surface, rather than reflecting extended development of the left surface. In the specimen of *A. cf. inflata* the slightly smaller right eye is the one with the larger number of files, again suggesting that it is that eye which is abnormal. Files 1–15 are normally developed, but file 16, while straight, does not extend to the top of the visual surface: it has the appearance of having been intercalated (Text-fig. 5E). Slight packing irregularities develop posterodorsally, because the upper parts of files 17 and 18 curve slightly forwards. I argue later in this paper that these eye asymmetries result from developmental abnormalities, although of course these could have been precipitated by injuries. Babcock (1993) recognized that sublethal injuries are more common on the right hand side of trilobites than on the left.

A. inflata resembles *A. downingiae*, a species which is more common and more widely distributed in the British Homerian. The number of specimens with well preserved visual surfaces, however, is small. The eyes of *A. downingiae* are generally larger than those of *A. inflata*, and were described in detail by Clarkson (1966a, p. 11). He distinguished two eye variants, basing his description on seven well preserved specimens (figures quoted below include some additional data collected by ATT and from Shergold 1966, p. 189). The more common form, Clarkson's eye variant A, has larger

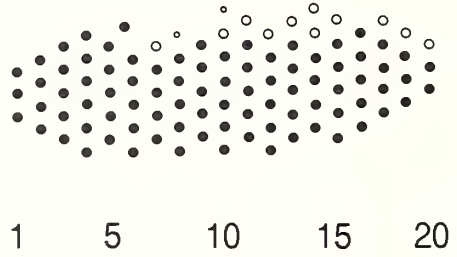
A



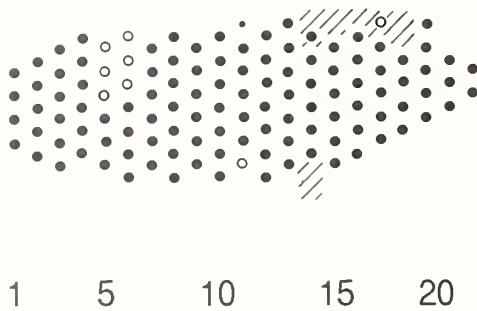
B



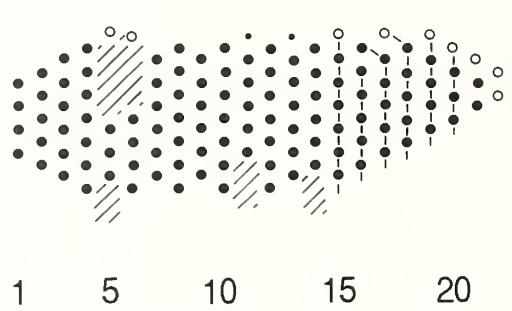
C



D



E



TEXT-FIG. 5. Schematic representation of visual surfaces in *Acaste inflata* Salter, 1864 and *A. cf. inflata*. Front of eye is to left; numbers below drawing denominate individual dorso-ventral files, counting from the front. A, *A. inflata*; plan of lens distribution in four surfaces of four specimens (OUM C559, C614, C617, NHM I1520). Numbers in boxes indicate the number of surfaces having that lens; ranges indicate uncertainty due to preservation. B-C, *A. inflata*; plan of lens distribution in left and right eyes of lectotype, OUM C9; Much

TABLE 1. Distribution of lenses in the visual surfaces of *Acaste* species, anterior of eyes to left. Top row shows number of lenses per file in *A. inflata* (left eye of OUM C614). Data below are counts from *A. downingiae* eye variant B (from Clarkson 1966a, table 1, p. 13; based on SM A28737 and A28741).

<i>A. inflata</i>	345	666	677	777	767	665	543	2
<i>A. downingiae</i>	{ 345	566	567	666	656	655	543	
	{ 345	677	778	787	777	676	654	32

eyes, with 22–25 files. The total number of lenses recorded ranges from 111 to 168, with files of 7 (8) alternating with 8 (9) at the maximum height of the visual field. Specimens of eye variant B have smaller eyes, containing 109–136 lenses arranged in 21–23 dorso-ventral files. At the maximum height of the visual field, files of 6 (7) lenses alternate with 7 (8). The two eye variants occur in collections made from a single locality and are otherwise similar morphologically.

The range of variation in eye variant B overlaps with that found in the generally smaller-eyed *A. inflata* (Table 1). These data indicate that lens patterns provide a less reliable guide to species identification in acastomorphs than Shergold (1966) believed.

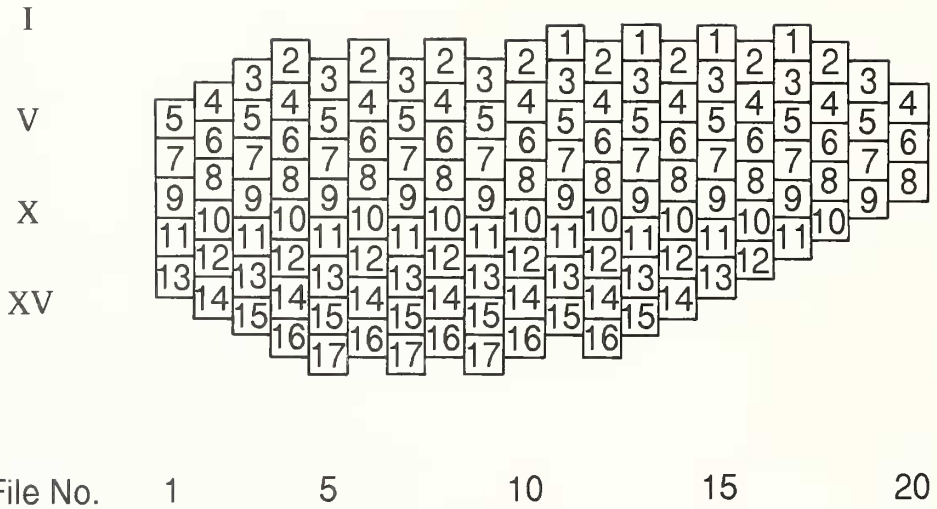
Given this overlap in morphology with a related species and the degree of variation known to occur in some other phacopines, I doubt that *A. downingiae* really displays dimorphism in its visual surface. It seems more likely that the apparent dimorphism reflects the small number of specimens on which the analysis was based: certainly, a significantly larger sample would be needed to demonstrate dimorphism convincingly. Dimorphism and polymorphism in eye morphology have been claimed quite widely in the Phacopina, and some cases were critically reviewed by Ramsköld and Werdelin (1991, p. 59). They concluded that some of the morphs may represent distinct taxa, whilst in other cases it is not known whether different morphs originally occurred at the same horizons. Among Silurian trilobites, the most convincing case of polymorphism was described by Siveter (1989) in his *Ananaspis* aff. *stokesii* (= *A. (s.l.) nuda* Salter, 1864; see Ramsköld and Werdelin 1991, p. 73), from western Ireland. In that species, a morph with 21? or 22 files with up to nine lenses in each co-occurs with a smaller-eyed form possessing 17–20 files, with a maximum of six lenses per file (Siveter 1989, p. 136, pl. 19). The differences in the visual surface are associated with other minor morphological contrasts.

DEVELOPMENT OF THE VISUAL SURFACE IN PHACOPINA

The existing state of knowledge was reviewed by Clarkson (1975, p. 13). Eyes first appear in the protaspis stage. They are anteriorly placed, and migrate posteriorly during ontogeny. The first lenses are emplaced in a generative zone lying directly below the palpebral margin, and these form a single horizontal row (the accessory upper horizontal row on Text-fig. 1). This generative zone has the form of an anteriorly expanding logarithmic spiral in plan view (Clarkson 1975, fig. 3a–c, p. 14). As the eye grows, the generative zone migrates downwards so that subsequent lenses are always emplaced below existing ones, at the bottom of the visual surface. Clarkson distinguished two components to the developmental programme: (1) growth of the generative zone; (2) lens

Wenlock Limestone Formation, Ledbury Railway Tunnel, Hereford and Worcester. Shaded circles indicate presence of lens in both eyes. D–E, *A. cf. inflata*; plan of lens distribution in left and right eyes of NMW 27.110.G998.3; Much Wenlock Limestone Formation, Dudley, West Midlands. Shaded circles indicate presence of lens in both eyes. Dashed lines in E indicate the traces of files 15–20: packing irregularities occur in this part of the eye.

Horizontal
Row No.



TEXT-FIG. 6. Schematic representation of visual surface in a paralectotype of *Eophacops musheni* (Salter). Front of eye is to left; numbers below drawing denominate individual dorso-ventral files, counting from the front. Roman numerals denote successive horizontal rows; boxes representing lenses are numbered accordingly. See text for discussion.

emplacement. He noted that lens addition may begin while the generative zone is still growing anteriorly, and used this to account for the accessory upper horizontal row of lenses in the rear part of the eye in dalmanitids. The patterns of variation described here further clarify the process of visual surface development in phacopine trilobites.

In the simplest case, several centres in the generative zone would become active simultaneously, thus creating a simple accessory upper horizontal row. The variation at the top of the visual field in *E. musheni* and *A. inflata* implies that initiation of lens emplacement was not synchronous in all individuals. Although a pattern of vertical files and horizontal rows could be constructed by an inclined generative zone, the pattern of lengthening of successive horizontal rows at the top of the visual surface described below indicates that the generative zone was orientated horizontally (i.e. at right angles to the file axes) during its descent. Additional active centres arose anteriorly and posteriorly as each new horizontal row was added: this would allow for the emplacement of new lenses as the visual surface expanded, and lenses in equivalent positions should be identifiable posteriorly and dorsally (Clarkson and Tripp 1982, p. 293). Text-figure 6 illustrates the inferred sequence of lens emplacement in a single specimen of *E. musheni*. Lens emplacement began posterodorsally, with the development of an accessory upper horizontal row of four lenses. In forming horizontal row II (eight lenses), the active section of the generative zone had extended anteriorly to a considerable extent, but to a much smaller degree posteriorly. By row IV, the maximum number of lenses (ten) was achieved. By this stage, the active section of the generative zone had expanded forward to its full extent, so that positionally equivalent lenses can be recognized in the upper anterior portion of the visual field (Text-fig. 2). An individual with eyes asymmetrical in terms of file number could be produced either by arrested development of the active section of the generative zone on one side, or by its continued extension on the other. This seems to have

occurred in the specimens of *E. nusheni* and *A. inflata*, and could account for the possession of additional files either anteriorly or posteriorly. The apparent intercalation of an additional, incomplete, file into one visual surface of the specimen of *A. cf. inflata*, implies the development of an additional centre of lens development within the active section of the generative zone during its downwards migration.

Horizontal rows IV to IX all contain ten lenses, so that the eye contains 20 files. Termination of lens emplacement began at the rear of the eye (row IX), and somewhat later at the front (row XIII), the anterior and posterior descending diagonal rows at the base of the eye indicating that emplacement persisted longest anteromedially (files 5–9). Again, variation in the timing of the termination of lens emplacement in different individuals would lead to the observed variation in lens patterns in the lower part of the eye.

The additional developmental instructions needed to produce the patterns documented are: initiation of lens emplacement along an active section of the generative zone; growth of this section to a maximum size and its differential development anteriorly; and termination of lens emplacement.

Initiation of lens emplacement. A trigger must have caused lens emplacement to begin in an active section of the generative zone. If initiation of an individual lens was controlled by the distance between adjacent lens centres, then lenses in each horizontal row would be equally spaced, and those in vertically adjacent horizontal rows would alternate: this automatically leads to hexagonal close packing and to the production of dorso-ventral files. A characteristic of certain Phacopina is that the lenses increase in size from top to bottom of the dorso-ventral files, reflecting increased spacing of lens centres through a constant arithmetic factor in successive horizontal rows (Clarkson 1975, p. 20; Pl. 1, fig. 3). This device allows areally efficient hexagonal close packing to be combined with arrangement of lenses in files and rows while the visual surface simultaneously expands outwards as well as downwards.

Fortey and Morris (1977) described variation in lens packing in *Phacops turco* aff. *praecedens* from the Eifelian of Morocco. Their sample is dominated by individuals whose eye lenses are emplaced on the cubic close packing system, although one specimen displays hexagonal close packing, and two show an intermediate arrangement. All specimens have clear dorso-ventral files. Evidently the regular arrangement of lenses was of greater importance to the animals than the efficiency of the packing system. In the case of the specimens showing cubic close packing, the retention of dorso-ventral files must reflect modification of the spacing factor between adjacent lens centres in successive horizontal rows.

Growth to a maximum size of the active section of the generative zone and its differential growth anteriorly. Differences in the number of lenses in the horizontal row results in eyes with different numbers of dorso-ventral files. The existence of individual specimens possessing eyes which differ in the number of files indicates that file number is not an expression of direct genetic control. Rather, it is a consequence of a developmental programme.

Termination of lens emplacement. Once initiated at the back of the eye, termination of lens emplacement progressed continuously. The maximum number of lenses in each dorso-ventral file is thus a consequence of the timing of onset of termination of lens emplacement and the number of files which occur (the latter, in turn, reflects the maximum number of lenses in a horizontal row).

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